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Armillaria xiaocaobaensis sp. nov. from China

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Abstract—A new wood-inhabiting fungal species from Yunnan Province, China, is proposed based on morphological and molecular characters. *Armillaria xiaocaobaensis* is characterized by a central stipe, striate to furrowed orange yellow to pinkish brown pileus surface, membranous annulus, and ellipsoid, a monomitic hyphal system with generative hyphae bearing simple septa, and slightly thick-walled basidiospores averaging 7.7 × 4.9 µm. TEF1 sequence analyses support *A. xiaocaobaensis* as a distinct taxon in *Armillaria*.

Key words—*Agaricales*, phylogenetic, *Physalacriaceae*, pathogenic fungi, taxonomy

Introduction

Species in *Armillaria* (Fr.) Staude (*Physalacriaceae, Basidiomycota*) are well known as important plant pathogens that can cause serious root diseases on diverse trees and woody plants, resulting in huge economic losses (Wargo & Shaw 1985, Baumgartner 2004, Lalande & al. 2018).

Armillaria includes approximately 40 species (Volk & Burdsall 1995, Kirk & al. 2008, Brazeel & al. 2012, Hood & Ramsfield 2016, Elías-Román & al. 2018) worldwide, and ten *Armillaria* species are currently recognized in China (Qin & al. 2000, 2007; Sun & al. 2003; Zhao & al. 2008; Coetzee & al. 2015; Guo & al. 2016).

Recent phylogenetic studies of *Armillaria* based on sequences of the internal transcribed spacer (ITS) region, the large subunit of nuclear

ribosomal RNA gene (nLSU), translation elongation factor 1-α (TEF1), and β-tubulin have greatly increased the number of identified fungal species and revealed the relationships among species in this genus (e.g., Maphosa & al. 2006, Hasegawa & al. 2010, Ross-Davis & al. 2012, Tsykun & al. 2013, Coetzee & al. 2015, Park & al. 2018). Lima & al. (2008) described one new South American species, *Armillaria paulensis* Capelari, based on morphology and ITS sequences that showed its closeness to *A. luteobubalina* Watling & Kile, while Brazee & al. (2012) introduced *A. altimontana* Brazee & al. in North America based on morphological and molecular phylogenetic evidence. In New Zealand, Hood & Ramsfield (2016) revealed *A. aotearoa* I.A. Hood & Ramsfield using morphology, interfertility cultures, and DNA sequence data. Guo & al. (2016) analyzed Chinese *Armillaria* samples using the sequences of ITS, TEF1 and β-tubulin gene, which revealed 15 phylogenetic lineages of *Armillaria* from China and showed that TEF1 was the most parsimony informative. Koch & al. (2017) resolved phylogeny and biogeography of *Armillaria*, *Desarmillaria* (Herink) R.A. Koch & Aime, and *Guyanagaster* T.W. Henkel & al. Elías-Román & al. (2018) described *A. mexicana* Elías-Román & al. based on morphology, DNA-sequence data (ITS, nLSU and TEF1), and phylogenetic analyses.

Our research on macrofungi in southern China revealed specimens that could not be assigned to any described species within *Armillaria*. The authors sampled previous research using the translation elongation factor-1 alpha gene (TEF1) sequences to explore the taxonomy and phylogeny of this undescribed species, proposed below as *Armillaria xiaocaobaensis*.

Materials & methods

Macroscopical descriptions were based on field notes. Color terms follow Petersen (1996). Dried material was examined microscopically using a compound microscope following Dai (2012). The following abbreviations were used: KOH = 5% potassium hydroxide, CB = cotton blue, CB– = acyanophilous, IKI = Melzer's reagent, IKI– = both inamyloid and nondextrinoid, L = mean spore length (arithmetic average of all spores), W = mean spore width (arithmetic average of all spores), Q = variation in the L/W ratios between the specimens studied, n (a/b) = number of spores (a) measured from given number (b) of specimens. The specimens studied are deposited at the herbarium of Southwest Forestry University, Kunming, China (SWFC).

Genomic DNA was extracted from dried specimens using the EZNA HP Fungal DNA Kit according to the manufacturer's instructions with some modifications. A small piece (about 30 mg) of dried fungal specimen was ground to powder with liquid nitrogen. The powder was transferred to a 1.5 mL centrifuge tube, suspended

in 0.4 mL of lysis buffer, and incubated in a 65 °C water bath for 60 min. After 0.4 mL phenol-chloroform (24:1) was added to the tube, the suspension was shaken vigorously. After centrifugation at 13,000 rpm for 5 min, 0.3 mL supernatant was transferred to a new tube and mixed with 0.45 ml binding buffer. The mixture was then transferred to an adsorbing column (AC) for centrifugation at 13,000 rpm for 0.5 min. Then, 0.5 mL inhibitor removal fluid was added in AC for a centrifugation at 12,000 rpm for 0.5 min. After washing twice with 0.5 mL washing buffer, the AC was transferred to a clean centrifuge tube, and 100 ml elution buffer was added to the middle of adsorbed film to elute the genomic DNA. TEF1 was amplified with primer pairs EF1-983F and EF1-2218R (Rehner 2001). The PCR procedure for TEF1 was as follows: initial denaturation at 94 °C for 1 min, followed by 35 cycles at 94 °C for 30 s, 59 °C for 1 min and 72 °C for 1.5 min, and a final extension of 72 °C for 10 min. The PCR products were purified and directly sequenced at Kunming Tsingke Biological Technology Limited Company. All newly generated sequences were deposited in GenBank (Table 1).

GeneCodes Sequencher 4.6 was used to edit the DNA sequence. Sequences were aligned in MAFFT 7 (https://mafft.cbrc.jp/alignment/server/index.html) using the "G-INS-I" strategy and manually adjusted in BioEdit (Hall 1999). The sequence alignment was deposited in TreeBase (submission ID 24610). *Oudemansiella cubensis* (Berk. & M.A. Curtis) R.H. Petersen and *Strobilurus esculentus* (Wulfen) Singer were used as outgroup to root trees following Koch & al. (2017) in the TEF1 analyses.

Phylogenetic analyses of the TEF1 sequences were performed using maximum parsimony, maximum likelihood, and Bayesian inference methods. Maximum parsimony (MP) analyses followed Zhao & Wu (2017), and tree construction was performed in PAUP* version 4.0b10 (Swofford 2002). All characters were equally weighted and gaps were treated as missing data. Trees were inferred using the heuristic search option with TBR branch swapping and 1000 random sequence additions. Max-trees were set to 5000, branches of zero length were collapsed, and all parsimonious trees were saved. Clade robustness was assessed using bootstrap (BT) analysis with 1000 replicates (Felsenstein 1985). Tree length (TL), consistency index (CI), retention index (RI), rescaled consistency index (RC), and homoplasy index (HI) were calculated for each Maximum Parsimonious Tree (MPT) generated. Sequences were analyzed using Maximum Likelihood (ML) with RAxML-HPC2 through the Cipres Science Gateway (www.phylo.org; Miller & al. 2009). Branch support (BS) for ML analysis was determined by 1000 bootstrap replicates.

MrModeltest 2.3 (Nylander 2004) was used to determine the best-fit evolution model for each data set for Bayesian inference (BI). Bayesian inference was calculated with MrBayes_3.1.2 using a general time reversible (GTR) model of DNA substitution and a gamma distribution rate variation across sites (Ronquist & Huelsenbeck 2003). Four Markov chains were run for 2 runs from random starting trees for 5 million generations (TEF1) and trees were sampled every 100 generations. The first 25% of the generations were discarded as burn-in. A majority

Table 1. Sequences used in the phylogenetic analyses; new sequences in **bold**.

Species	Sample no.	GenBank no. TEF1	Reference
Armillaria altimontana	D 82	JN944611	Brazee & al. 2012
	POR 100	JN944606	Brazee & al. 2012
A. aotearoa	NZFRIM 5283	KU295542	Hood & Ramsfield 2016
A. borealis	HKAS 56108	KT822293	Guo & al. 2016
	HKAS 76263	KT822294	Guo & al. 2016
A. calvescens	ST 17	JF895836	Brazee & al. 2011
	ST 18	JF895837	Brazee & al. 2011
	ST 3	JF895835	Brazee & al. 2011
A. cepistipes	F 011081	KT822416	Guo & al. 2016
	S 20	JF313116	Brazee & al. 2011
A. fumosa	CMW 4955	DQ435646	Maphosa & al. 2006
A. fuscipes	CMW 3164	DQ435621	Maphosa & al. 2006
	CMW 4953	DQ435622	Maphosa & al. 2006
A. gallica	M 70	HQ432899	Direct Submission
	ST 22	HQ432897	Elías-Román & al. 2018
A. gemina	ST 8	JF313136	Brazee & al. 2011
	ST11A	JF313133	Brazee & al. 2011
A. heimii	K 59	FJ618644	Elías-Román & al. 2018
	PH 8724	FJ618651	Elías-Román & al. 2018
A. hinnulea	CMW 4980	DQ435648	Maphosa& al. 2006
A. limonea	CMW 4680	DQ435655	Maphosa& al. 2006
	CMW 4991	DQ435656	Maphosa & al. 2006
	Plim 8466	FJ618654	Elías-Román & al. 2018
A. luteobubalina	CMW 4977	DQ435657	Maphosa & al. 2006
	CMW 8876	DQ435658	Maphosa & al. 2006
A. mellea	CMW 4613	DQ435637	Maphosa & al. 2006
	G 0405414	KT822345	Guo & al. 2016
	MEX 74	KC111011	Elías-Román & al. 2018
A. mexicana	MEX 85	KR061313	Elías-Román & al. 2018
	MEX 87	KR061314	Elías-Román & al. 2018
	MEX 88	KR061315	Elías-Román & al. 2018
A. nabsnona	C 21	JF313119	Elías-Román & al. 2018
	HKAS 85523	KT822411	Guo & al. 2016
A. novae-zelandiae	CMW 4722	DQ435652	Maphosa & al. 2006
	CMW 5448	DQ435653	Maphosa & al. 2006
A. ostoyae	EC4	JF746925	Brazee & al. 2011
	EC 5	JF746926	Brazee & al. 2011
A. pallidula	3626	FJ618665	Elías-Román & al. 2018
	CMW 4971	DQ435647	Maphosa & al. 2006
A. puiggarii	MCA 3111	KU289104	Koch & al. 2017
	TH 9751	KU289113	Koch & al. 2017

Species	Sample no.	GenBank no. TEF1	Reference
A. sinapina	A 9601539	KT822422	Guo & al. 2016
	M 50	JF313114	Brazee & al. 2011
	ST 12	JF313132	Brazee & al. 2011
	ST 13	JF313131	Brazee & al. 2011
A. solidipes	P 1404	JF313140	Brazee & al. 2011
	ST 2	JF313139	Brazee & al. 2011
A. xiaocaobaensis	**SWFC 12637**	**MN298777**	**This study**
	SWFC 12638[T]	**MN298778**	**This study**
	SWFC 12639	**MN298779**	**This study**
Desarmillaria ectypa	7001113	KT822438	Guo & al. 2016
	CMW 15693	FJ875698	Koch & al. 2017
	MY 84941	FJ618643	Koch & al. 2017
D. tabescens	90158	KT822439	Koch & al. 2017
	I 9912213	KT822441	Guo & al. 2016
	PT 8412	FJ618658	Koch & al. 2017
Guyanagaster necrorhizus	G 314	KU289110	Koch & al. 2017
	G 352	KU289109	Koch & al. 2017
	MCA 3950	KU289107	Koch & al. 2017
	RAK 31	KU289108	Koch & al. 2017
Oudemansiella cubensis	MCA 5434	KU289105	Koch & al. 2017
Strobilurus esculentus	Yang 5027	KF530581	Koch & al. 2017

rule consensus tree of all remaining trees was calculated. Branches that received bootstrap support for maximum likelihood (BS), maximum parsimony (BT), and Bayesian posterior probabilities (BPP) greater than or equal to 75% (BS, BT) and 0.95 (BPP) were considered significantly supported.

Molecular phylogeny

The TEF1 dataset included sequences from 62 fungal specimens representing 29 species (Table 1). The alignment comprised 544 characters of which 312 characters were constant, 29 variable and parsimony-uninformative, and 203 parsimony-informative. Maximum parsimony analysis yielded four equally parsimonious trees (TL = 728, CI = 0.496, HI = 0.504, RI = 0.781, RC = 0.387). Best model for the TEF1 dataset estimated and applied in the Bayesian analysis: GTR+I+G. Bayesian analysis and ML analysis resulted in a similar topology as MP analysis, with an average standard deviation of split frequencies = 0.003738 (BI).

The phylogeny inferred from TEF1 sequences placed *Armillaria xiaocaobaensis* in a monophyletic lineage with strong support (BS = 100%; BT = 100%; BPP = 1).

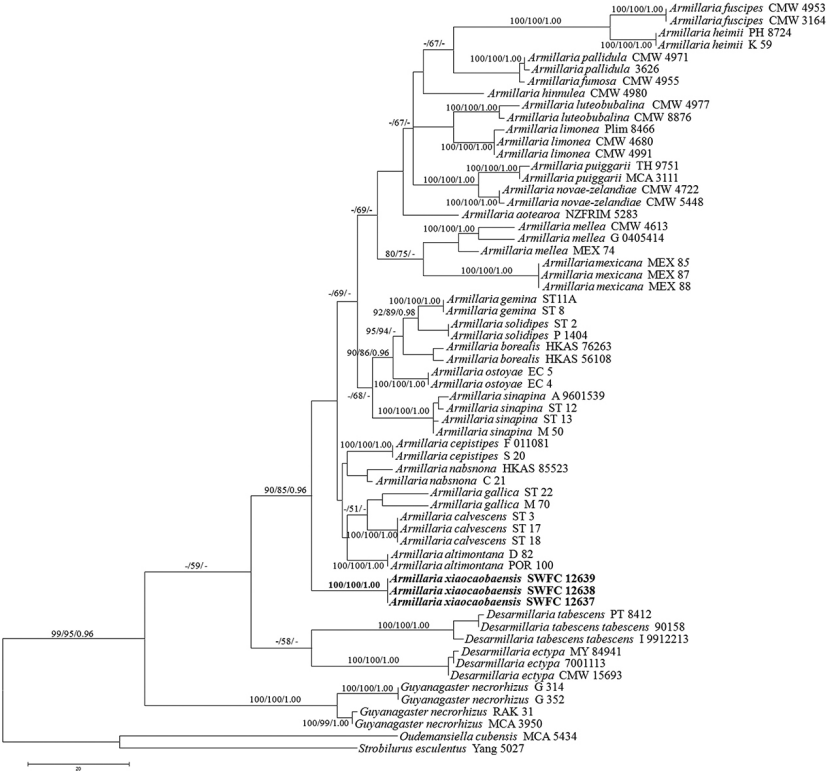

Fig. 1. Maximum parsimony strict consensus tree illustrating the phylogeny of *Armillaria xiaocaobaensis* and related species based on TEF1 sequences. Branches are labeled with maximum likelihood bootstrap >70%, parsimony bootstrap proportions >50%, and Bayesian posterior probabilities >0.95.

Taxonomy

Armillaria xiaocaobaensis Jia H. Peng & C.L. Zhao, **sp. nov.** Figs 2, 3

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Differs from *Armillaria altimontana* by its centrally stipitate basidiomes with striate to furrowed, orange yellow to pinkish brown pileus surface, membranous annulus, and smaller, ellipsoid, thin-walled basidiospores.

Type: China. Yunnan Province: Zhaotong, Yiliang County, Xiaocaoba Town, on angiosperm trunk, 19 April 2019, Jia-Hua Peng (**Holotype**, SWFC 0012638; GenBank MN298777).

Etymology: *xiaocaobaensis* (Lat.) refers to the locality (Xiaocaoba Town) of the type specimen.

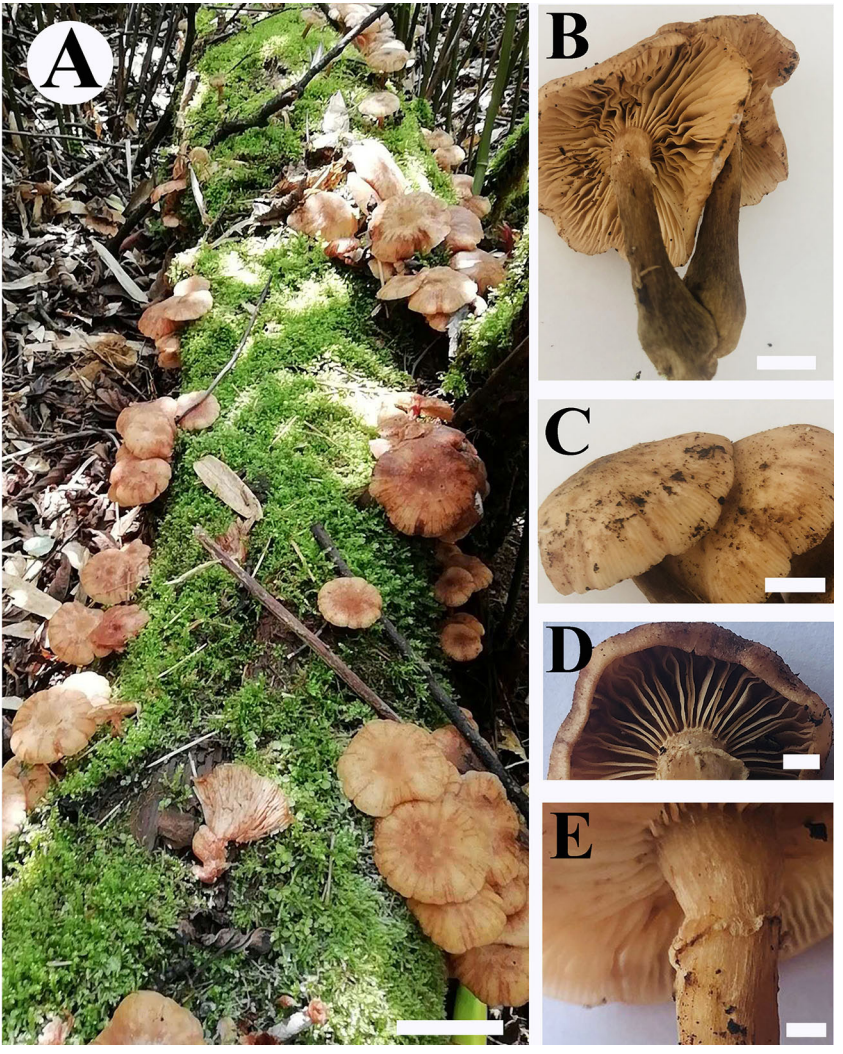

Fig. 2. *Armillaria xiaocaobaensis* (holotype, SWFC 0012638).
Scale bars: A = 4 cm; B, C = 1 cm; D = 5 mm; E = 2 mm.

Basidiomata pileate, centrally stipitate, caespitose. Pileus 30–40 mm diam., umbonate, convex to plano-convex, orbicular in apical view, margin deflexed to lobed, pileus surface striate to furrowed, orange yellow to pinkish brown in the center, and pale yellow to pale brown at margin. Lamellae 5 mm deep, close,

decurrent, adnate, edges entire, buff to light yellow. Lamellulae attenuate, edges entire, multi-tiered. Annulus 4–5 mm wide, superior, persistent, membranous, appressed to stipe, buff to light yellow. Stipe 35–60 × 4–6 mm, central, cylindrical, solid, light yellow to pale pinkish brown to brown to black toward the base in fresh specimens, base bulbous. Rhizomorphs absent. Taste and odor not tested. Spore print white.

Basidiospores ellipsoid, hyaline, slightly thick-walled, smooth, IKI–, CB–, (6.5–)7–8.5(–9) × 4–5.5(–6) µm, L = 7.74 µm, W = 4.93 µm, Q = 1.53–1.64 (n = 90/3). Basidia barrel-shaped to clavate, with 2–4 sterigmata and a simple basal septum, 20–28 × 5.5–8.5 µm; basidioles dominant, mostly clavate but slightly smaller than basidia. Hymenophoral trama generative hyphae bearing simple septa, hyaline, thin-walled, unbranched, 5–8 µm in diam. Cystidia none observed. Pileipellis hyphae hyaline, thin-walled, unbranched, 8–13 µm diam. Context 100–150 µm wide, hyphae hyaline, thin-walled, unbranched, 6–10 µm diam. Stipitipellis hyphae hyaline, thin-walled, unbranched, 3.5–5.5 µm diam. Clamp connections absent.

Additional specimens examined: **CHINA. Yunnan province. Zhaotong:** Yiliang County, Xiaocaoba Town, on angiosperm trunk, 19 June 2019, Jia-Hua Peng (SWFC 0012637; SWFC 0012639).

Discussion

Phylogenetic analyses and morphological characters support *Armillaria xiaocaobaensis* as a new species.

In the TEF1 analyses (Fig. 1), *A. xiaocaobaensis* formed a monophyletic lineage with strong support (BS = 100%; BT = 100%; BPP = 1) and grouped with *Armillaria altimontana*, *A. calvescens* Bérubé & Dessur., *A. cepistipes* Velen., *A. gallica* Marxm. & Romagn., and *A. nabsnona* T.J. Volk & Burds. However, morphologically *A. altimontana* differs from *A. xiaocaobaensis* by its tricholomatoid basidiomata with a reddish brown pileus bearing cream scales and short fibrils (Brazee & al. 2012) and from *A. calvescens* by the presence of pileus scales and fibrils, and larger basidiospores (8.5–10 × 5–7 µm; Bérubé & Dessureault 1989). *Armillaria cepistipes* differs in its yellow ochraceous to ochraceous brown pileus, longer stipe (100 × 9–11 mm), and larger basidia (29–45 × 8.5–11 µm; Antonín & al. 2009); and *A. gallica* by the presence of dark brown to pinkish brown pileus, long fibrillose pileus scales, and ellipsoid to amygdaloid, larger basidiospores (7.5–11 ×5–6.5 µm; Antonín & al. 2009). *Armillaria nabsnona* has a hygrophanous pileus with a white context and larger basidiospores (8–10 × 5.5–6.5 µm; Volk & al. 1996).

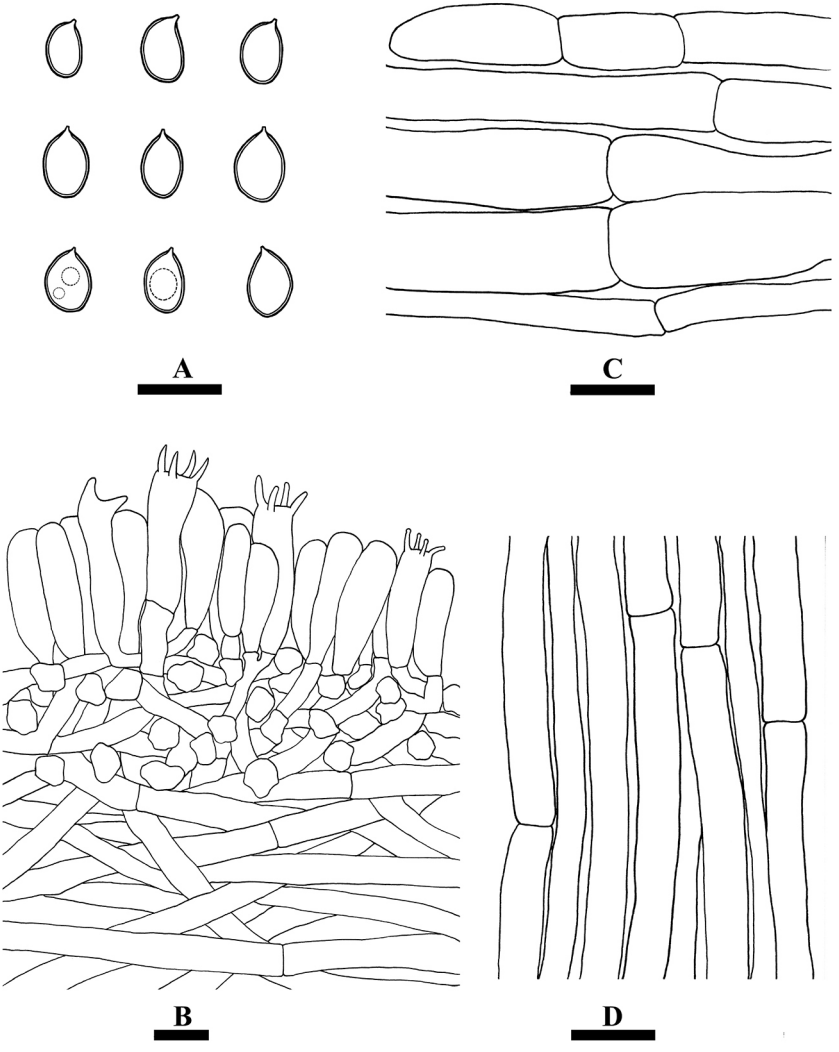

Fig. 3. Microscopic structures of *Armillaria xiaocaobaensis* (drawn from the holotype, SWFC 0012638). A. Basidiospores; B. Section of hymenium; C. Pileipellis; D. Stipitipellis. Scale bars: A–D = 10 μm.

Armillaria xiaocaobaensis is close to *Desarmillaria*, a member in the sister genus based on the molecular data (Fig. 1). *Desarmillaria* is distinguished morphologically from *Armillaria* by the absence of an annulus (Koch & al. 2017).

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